USING REPEATED MEASURES TO ESTIMATE CRITICAL THRESHOLDS AND CLASSIFY STATES IN SHALLOW LAKES

Kelsey Vitense[1], John Fieberg[1], Mark A. Hanson, Brian R. Herwig[2], and Kyle D. Zimmer[3]

SUMMARY OF FINDINGS

Shallow lakes can quickly transition between 2 alternative stable states: a clear state dominated by submerged aquatic vegetation, which provides critical habitat for waterfowl, and a turbid state characterized by extreme algal blooms, sparse submerged vascular plants, and poor habitat quality. Theoretical models suggest that critical nutrient thresholds differentiate highly resilient clear lakes, lakes that may switch between clear and turbid states following system perturbations (e.g., weather events, zooplankton community changes), and highly resilient turbid lakes. Lake managers need decision tools to help guide and prioritize future lake projects. We are developing models to identify combinations of factors responsible for lake deterioration, to assess management potential of individual lakes, and to help gauge the relative risk of state transitions for shallow lakes. We have developed an integrated modeling framework to (1) identify critical nutrient (TP) thresholds, (2) classify attracting lake states, and (3) estimate state-dependent relationships between TP and measures of algal abundance (Chla). Here, we provide a modified version of our model that utilizes repeated lake measurements. We plan to use these and other study products to develop an interactive decision support tool that will help managers identify lakes needing special protection, fine-tune management needs of individual lakes, and rank lakes as candidates for future lake management efforts.

INTRODUCTION

Shallow lakes generally conform to one of 2 alternative stable states: a clear state with primary production dominated by submerged aquatic vegetation (SAV) and a turbid state with phytoplankton dominating over SAV (Scheffer et al. 1993). Excessive nutrient inputs from current and historical land use, food web-mediated influences and sediment disturbance caused by planktivorous and benthivorous fish, and wind all drive transitions to, and affect the resilience of, turbid states (Scheffer 1998). Shallow lakes with high nutrient levels are prone to explosive, unhealthy phytoplankton "blooms," especially when phosphorus (P) is readily available (Scheffer 1998). Submerged aquatic vegetation, which sustains the diverse invertebrate communities that provide important food sources for waterfowl, is reduced in this turbid, algae-dominated state (Hargeby et al. 1994). Parasites associated with amphibian malformations likely have higher prevalence in turbid lakes (Johnson and Chase 2004) and nitrogen may accumulate at higher rates (Zimmer et al. 2003). It is not surprising that key goals for shallow lake management are to prevent shifts from clear to turbid states, to induce shifts from turbid to clear states, and to maintain the natural resilience of clear-water shallow lakes.

[1]Department of Fish, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN
[2]Fisheries Research, Minnesota Department of Natural Resources, Bemidji, MN
[3]Department of Biology, University of St. Thomas, St. Paul, MN

Complex ecological and physical mechanisms are responsible for maintaining the stability of each alternative state, such as competition between primary producers. When SAV declines, phytoplankton abundance typically increases, limiting light reaching the lake bottom and further restricting SAV in a positive-feedback loop (Scheffer et al. 1993). Additionally, when SAV is sparse, sediments are easily disturbed by benthivorous fish and waves. Suspended sediments further increase turbidity, and mobilized P stimulates even higher phytoplankton growth rates (Scheffer 1998). In contrast, in clear-state lakes, SAV remains widely distributed and helps maintain water clarity by stabilizing sediments and taking up nutrients (Søndergaard et al. 2003). Charophytes (*Chara*) often accompany clear-water conditions in Minnesota lakes and are believed to release algal toxins (Berger and Schagerl 2004) and provide refuge for zooplankton, which may further reduce the phytoplankton population and help stabilize clear-water conditions.

Shallow lakes are notoriously difficult to restore after shifting from clear to turbid states, with turbid conditions frequently returning within 5-10 years following lake management (Søndergaard et al. 2007, Hanson et al. 2017). Theoretical models are useful for understanding how nutrients influence whether lakes will tend toward turbid or clear water states in the long run. For example, Figure 1 shows a bifurcation diagram derived from a model describing shallow lake dynamics. At low nutrient levels (left of “tip down” threshold in Figure 1), lakes can only exist in the clear stable state. At high nutrient levels (right of the “tip up” threshold in Figure 1), lakes only exist in the turbid state. In between these 2 thresholds, the system exhibits hysteresis in which 2 different steady states are possible under the same nutrient conditions, depending on whether the initial turbidity levels lie above or below the unstable state in this region of bistability (dashed line in Figure 1).

The bifurcation diagram is also useful for understanding temporal dynamics and shifts between stable states. If a lake is in the clear state with high SAV (lower solid line) and nutrient input increases beyond the “tip up” bifurcation point, the lake will likely transition quickly to the turbid state with low SAV (upper solid line). Once SAV is lost, the internal loading of nutrients increases and becomes hard to control, and external nutrient loading must be substantially reduced to the lower “tip down” bifurcation point to reverse the state shift (Scheffer and Carpenter 2003). In practice, such drastic nutrient reduction may not be possible or may only be accomplished over long time periods. Alternatively, managers may attempt to induce a state shift by forcing the system across the unstable line, e.g., by decreasing the planktivore and benthivore populations with rotenone (if nutrients can at least be reduced to the region of bistability) (Jeppesen et al. 2009). These resulting transitions are typically short-lived, however, because perturbations to the system (e.g., fish colonization, destruction of submerged vegetation) can force the lake back to the turbid state. For instance, Lake Christina, a large shallow lake in Minnesota, has been rehabilitated with fish toxicants three times in recent decades in an effort to improve habitat quality for migrating waterfowl. In each case, improved water quality and clear-state characteristics followed lake management, but the lake persistently transitioned back to turbid conditions 5-10 years after treatment (Hanson and Butler 1994, Hansel-Welch et al. 2003, Hobbs et al. 2012). Clear water conditions in Danish and Dutch lakes have also been observed to start deteriorating five years following biomanipulation (Meijer et al. 1994). Similarly, Hanson et al. (2017) showed that 8 shallow lakes in Minnesota did not transition to stable clear-state conditions during a period 2-4 years after management. Returns to turbid conditions following biomanipulation suggest that some shallow lakes may have nutrient levels beyond the “tip up” threshold in Figure 1 where only the turbid state is possible, or that observed clear states may have little ecological resilience such that small perturbations easily push the lakes back into the basin of attraction of the turbid state. These patterns are also consistent with paleolimnological findings of Ramstack Hobbs et al. (2016) who suggested that some shallow Minnesota lakes never recovered after crossing from clear- to turbid-state ecological regimes.

Failed attempts to manage turbid lakes illustrate that managers need better tools to predict whether their efforts will maintain clear conditions in high quality lakes, whether clear lakes are approaching thresholds and thus are likely to transition to turbid conditions, or if management will succeed in improving highly deteriorated lakes. Theoretical models and empirical studies suggest that we need to more accurately predict implications of changing nutrient levels and biological community features on attracting states and the likelihood that lakes will flip to turbid states. Such information will help managers prevent undesirable state shifts in shallow lakes, identify lakes that are good candidates for rehabilitation, and inform future conservation strategies for both lakes and adjacent watershed areas.

As a first step toward addressing these information gaps, we have successfully developed an integrated modeling framework (Vitense et al. 2016) using Bayesian latent variable regression (BLR) models to: 1) classify attracting lake states (clear vs. turbid); 2) estimate deterministic steady state relationships between total phosphorus (TP) and chlorophyll *a* (Chla); and 3) identify critical TP thresholds that differentiate highly resilient clear lakes, lakes that can transition between clear and turbid states following perturbations, and highly resilient turbid lakes. However, our previously developed BLR model assumes each lake has been sampled only once, but it is common for researchers to have 1-3 years of data for a set of lakes.

Several possibilities exist for handling multiyear data for a population of lakes within our framework: 1) within-lake observations could be assumed to be independent after conditioning on TP and state, and data could simply be pooled (similar to Wang et al. (2014)); 2) the BLR model can be fit separately to each year of data and then summarized across years (similar to Zimmer et al. (2009)); 3) correlated errors for repeated lake measurements can be built into the BLR model; e.g., a multivariate normal distribution could be used to describe the distribution of Chla with state-dependent within-lake correlated errors specified via a non-diagonal variance-covariance matrix; 4) a hierarchical approach can be employed with lake-level regression coefficients assumed to be random variables arising from a population-level distribution; 5) state transitions could be built into the model to create a hidden Markov model for individual lake dynamics. The most appropriate approach will likely depend on the data and underlying research questions or intended use of the model.

We illustrate options 2 and 4 here – i.e., we summarize separate model fits to each year of data, and we also fit a model that includes random intercepts in the logistic regression between SAV and latent state. We discuss advantages and disadvantages of both approaches, but we ultimately find that threshold estimates and conclusions for our set of lakes in Minnesota are similar for both approaches.

METHODS

Data

The MDNR surveyed 130 lakes once in July during each of three consecutive years, 2009-2011. Measures of TP (μg/L), Chla concentration (μg/L), and SAV abundance (kg/sample) were obtained in each year. Nine lakes were sampled in only one or two years, and all lakes had maximum depths less than 5 m. Water samples for TP were collected at two stations in each lake-year and frozen until analysis with persulfate digestion and ascorbic acid colorimetry. Two samples for Chla were collected at the same time and place as TP by filtering water through GF/F filters. The filters were frozen until analysis for Chla by acetone extraction and flourometric analysis. The average Chla and TP values for each lake-year were used for analysis.

Submersed aquatic macrophytes were sampled with a weighted plant rake using methods modified from Deppe & Lathrop (1992). Plants were sampled at 15 stations in each lake by dragging the rake across 3 m of lake bottom and weighing plant biomass (wet weights) collected on the rake. The average plant biomass across the 15 stations for each lake-year was used for analysis.

Bayesian Latent Variable Regression (BLR) Model

Our BLR model describes relationships between the natural logarithms of TP and Chla with linear models with state-dependent intercepts, slopes, and normally distributed errors (Equations 1-3). Lake state (S_i) is estimated as a latent variable that follows a Bernoulli distribution (Equation 4). The probability that lake *i* is in the turbid state (denoted by S_i=1) depends on both its TP and SAV values (Equation 5). If the lake's TP level falls below the lower TP threshold (π_1 on the log scale), its probability of being turbid is 0; i.e., the lake is classified as clear. If the lake's TP level falls above the upper TP threshold (π_2 on the log scale), its probability of being turbid is 1; i.e., the lake is classified as turbid. If the lake's TP level falls between the thresholds, logistic regression is used to model its probability of being turbid as a function of SAV abundance.

$$\log(Chla_i) \sim N(\mu_i, \sigma_i^2) \tag{1}$$

$$\mu_i = a_0 + \tau S_i + b_0(1-S_i)\log(TP_i) + b_1 S_i \log(TP_i) \tag{2}$$

$$\sigma_i = \sigma_0(1-S_i) + \sigma_1 S_i \tag{3}$$

$$S_i \sim Bern(p_i),\ \mathrm{S}_i = \begin{cases} 0, & \text{if lake } i \text{ is clear} \\ 1, & \text{if lake } i \text{ is turbid} \end{cases} \tag{4}$$

$$p_i = P(\text{turbid}) = \begin{cases} 0, & \text{if } \log(TP_i) < \pi_1 \\ \text{logit}^{-1}(\gamma_0 + \gamma_1 \times SAV_i), & \text{if } \pi_1 \le \log(TP_i) \le \pi_2 \\ 1, & \log(TP_i) > \pi_2 \end{cases} \tag{5}$$

We chose priors that ensured the slopes describing the relationships between Chla and TP were positive and that the probability of a lake being turbid decreased as its abundance of SAV increased. All other priors were weakly informative:

$$\begin{aligned} &a_0 \sim \mathcal{N}(0,10^2); \quad \tau \sim \mathcal{N}(0,3.16^2); \quad b_0,\ b_1 \sim Unif(0,10); \ \ \sigma_0,\ \sigma_1 \sim Unif(0,20) \\ &\gamma_0 \sim \mathcal{N}(0,10^2); \ -\gamma_1 \sim \ln\mathcal{N}(0.5,1); \ \pi_1,\ \pi_2 \sim Unif(0,6.5) \end{aligned} \tag{6}$$

Finally, we included a constraint to force the line connecting the turbid line at $\ln(TP_i) = \pi_1$ to the clear line at $\ln(TP_i) = \pi_2$ to have a negative or flat slope to reflect the "S"-shape of Figure 1:

$$(\tau + b_1\pi_1 - b_0\pi_2)/(\pi_1 - \pi_2) \le 0 \tag{7}$$

Fitting and Summarizing Separate Model Fits

We fit the BLR model above to each of the three years of Minnesota shallow lake data separately. We ran the models in JAGS (Plummer 2003) using the R package 'R2jags' (Su and Yajima 2015). For each year, we ran three chains for 10,000,000 iterations with a burn-in of 2,000,000 and thinning rate of 2,400. We examined convergence using trace plots and the Gelman-Rubin convergence statistic (Gelman and Rubin 1992). Within each year, we classified a lake as turbid (clear) if over half of the sampled states from the Markov chain Monte Carlo (MCMC) chains were turbid (clear) for that lake. We estimated regression coefficients and TP thresholds using medians and modes of the posterior distributions, respectively, and computed 95% credible intervals for the regression coefficients and TP thresholds for each year.

We summarized the fits across the 3 different years in a heat map of the state classifications in all 3 years, and we used median TP threshold estimates across the 3 fits as overall TP threshold estimates.

Random Parameter Extension to BLR Model

Our BLR model is flexible, and random parameters can be incorporated to account for correlation among repeated measurements or to allow certain relationships to vary among lakes. We highlight a model that includes random intercepts in the logistic regression describing how the probability a lake is turbid changes with SAV (Equation 12). This model formulation reflects that the lakes' inherent chance of being turbid in the bistable region may vary because of factors not accounted for here (e.g., zooplankton community characteristics), but changes in SAV abundance are assumed to have the same effect on the probability of being turbid for all lakes (i.e., γ_1 in Equation 12 is a fixed effect). The random logistic intercept model we fit is formulated as follows, where *i, j* denotes the *j*th observation from lake *i*:

$$\log(Chla_{i,j}) \sim N(\mu_{i,j}, \sigma_{i,j}{}^2) \qquad (8)$$

$$\mu_{i,j} = a_0 + \tau S_{i,j} + b_0(1 - S_{i,j})\log(TP_{i,j}) + b_1 S_{i,j}\log(TP_{i,j}) \qquad (9)$$

$$\sigma_{i,j} = \sigma_0(1 - S_{i,j}) + \sigma_1 S_{i,j} \qquad (10)$$

$$S_{i,j} \sim Bern(p_{i,j}),\ \mathrm{S}_{i,j} = \begin{cases} 0, & \text{if observation } j \text{ for lake } i \text{ is clear} \\ 1, & \text{if observation } j \text{ for lake } i \text{ is turbid} \end{cases} \qquad (11)$$

$$p_{i,j} = P(\text{turbid}) = \begin{cases} 0, & \text{if } \log(TP_{i,j}) < \pi_1 \\ \text{logit}^{-1}(\gamma_{0,i} + \gamma_1 \times SAV_{i,j}), & \text{if } \pi_1 \le \log(TP_{i,j}) \le \pi_2 \\ 1, & \log(TP_{i,j}) > \pi_2 \end{cases} \qquad (12)$$

$$(\tau + b_1\pi_1 - b_0\pi_2)/(\pi_1 - \pi_2) \le 0 \qquad (13)$$

$$\begin{array}{lll} a_0 \sim \mathcal{N}(0,10^2); & \tau \sim \mathcal{N}(0,3.16^2); & b_0,\ b_1 \sim Unif(0,10) \\ \sigma_0,\ \sigma_1 \sim Unif(0,20); & \pi_1,\ \pi_2 \sim Unif(0,6.5); & -\gamma_1 \sim \ln\mathcal{N}(0.5,1) \\ \gamma_{0,i} \sim \mathcal{N}(\mu_{\gamma_0}, \sigma^2_{\gamma_0}); & \mu_{\gamma_0} \sim \mathcal{N}(0,10^2); & \sigma_{\gamma_0} \sim Unif(0,10); \end{array} \qquad (14)$$

We ran the random logistic intercept model in JAGS, examining the model for convergence. We computed parameter estimates and state classifications using the same approach outlined above. Chains were run for 1,000,000 iterations with a burn-in of 200,000 and thinning rate of 240.

RESULTS

The BLR model produced reasonable fits to each of the 3 years of shallow lake data treated separately and together (Figure 2). The fitted models resemble bifurcation diagrams with no evidence for lack of convergence.

The separate fits to the 3 years of data depict sampling variability between years. The heat map of state classifications across the 3 years (Figure 3) suggests that an approximate Chla threshold of 20 μg/L separates clear and turbid lakes in the bistable region. Indeed, roughly equal proportions of clear and turbid lake-years in the bistable region are divided by a Chla threshold of 19.9 μg/L. Across all lake-years, 53.7% of lake-years fall below the median lower TP threshold (49.97 μg/L), 43.7% fall in the bistable region, and 2.6% fall above the median upper TP threshold (366.36 μg/L). Across the 3 fits, 64.6% of lakes were classified as clear in all available years, 15.4% were turbid in all available years, and 20% transitioned at least once.

TP threshold posterior distributions and credible intervals are narrower for the random logistic intercept model compared to the separate fits (Table 1, Figure 2). We note that the upper TP threshold estimate for the random logistic intercept model is reduced to ~355 μg/L from ~437 μg/L if one influential observation from year 2009 is removed. For the random logistic model, the estimated unstable line ranges over Chla levels 15.0-19.9 μg/L. Additionally, roughly equal proportions of clear and turbid lake-years in the bistable region are divided by a Chla value of 19.8 μg/L, which is similar to the Chla threshold estimated using the 3 separate fits. For TP threshold estimates from the random logistic intercept model, 50.3% of lake-years fall below the lower threshold estimate (44.29 μg/L), 47.9% fall in the bistable region, and 1.9% fall above the upper threshold estimate (437.03 μg/L). Additionally, 65.4% of lakes were clear in all available years, 13.8% were turbid in all available years, and 20.8% transitioned at least once for classifications from the random logistic intercept model. These proportions are similar to those using classifications and median threshold estimates from the separate fits to the 3 different years.

DISCUSSION

Our Bayesian latent variable model (BLR) provides a formal modeling framework that can be adapted to allow for additional data features, such as repeated measures or more extensive time series. We illustrated both how separate model fits across different years can be summarized, as well as how multi-year data can be aggregated and the model extended to incorporate random parameters. The hierarchical modeling approach has the advantage of providing a single model fit for multi-year data and narrower TP threshold posterior distributions compared to the separate yearly model fits. However, summarizing across separate yearly fits reduces the influence of outlying data points and elucidates sampling variability between years. Future researchers may decide whether and which random parameters are appropriate for inclusion given their data and study systems.

Critical threshold estimates were similar, regardless of which approach was used. Chla levels of 19.8-19.9 μg/L separated clear and turbid lakes in the estimated bistable region into roughly equal proportions of clear lakes falling below and turbid lakes falling above these values for both approaches. The lower TP threshold estimates were also similar. The upper threshold estimate of the random logistic BLR model is similar to the median estimate of the separate yearly fits if one influential observation from 2009 is removed when fitting the hierarchical model; otherwise, the upper threshold for the hierarchical model is similar to the estimate in year 2009.

These threshold estimates provide important information to help managers make decisions about whether and how to treat different shallow lakes, and also help to define realistic expectations when attempting to rehabilitate a lake. Shallow lakes with TP levels below the lower estimated critical TP threshold may be deemed high priority clear lakes, with efforts focused on protecting adjacent watersheds or other features contributing to their pristine conditions. Indeed, the majority of the lakes in our study are highly stable clear lakes. On the other end, lakes with TP levels that are frequently above the upper TP threshold can be considered lower priority turbid lakes. The internal P loads can be so great in these lakes because of historically high nutrient inputs that the lakes will persistently return to turbid water conditions following management actions (Hobbs et al. 2012, Hanson et al. 2017, Ramstack Hobbs et al. 2016). Fortunately, a very low proportion of lakes in our study fall in this category. Finally, lakes that tend to fall in between the two thresholds are those for which active management is likely to be most practical, and our results suggest that 44-48% of the lake-years in our study fell in the bistable region. Lakes that tend to exist in this bistable region are highly dynamic, and managers may force these lakes from the turbid to clear stable state through actions such as biomanipulation of fish stocks or water level drawdowns. Additionally, the relative resilience of different lakes in the bistable region can be used to help prioritize lakes for management. For example, lakes can be placed on an estimated bifurcation diagram, and resilience can be estimated by each lake's proximity to TP thresholds or as the estimated distance between a lake's steady state and the unstable line or critical Chla threshold.

Finally, the BLR framework can be modified to include state transitions in which the trajectories of lakes crossing thresholds are directly modeled, which would likely allow for better identification of critical nutrient thresholds. Future research will be focused on model extensions for lake transitions to understand key factors driving changes to lake nutrient levels and top-down influences (e.g., fish and invertebrates) that drive regime shifts. These models will help to further refine predictions regarding which lakes are most likely to undergo successful rehabilitations and help to prioritize lakes for management.

ACKNOWLEDGMENTS

This project was funded in part by the Wildlife Restoration (Pittman-Robertson) Program.

LITERATURE CITED

Berger, J., and M. Schagerl. 2004. Allelopathic activity of Characeae. Biologia 59:9–15.

Deppe, E. R. and R. C. Lathrop. 1992. A comparison of two rake sampling techniques for sampling aquatic macrophytes. Wisconsin Department of Natural Resources, Findings #32, PUBL-RS-732-92.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.

Hansel-Welch, N., M. G. Butler, T. J. Carlson, and M. A. Hanson. 2003. Changes in macrophyte community structure in Lake Christina (Minnesota), a large shallow lake, following biomanipulation. Aquatic Botany 75:323–337.

Hanson, M. A., and M. C. Butler. 1994. Responses of plankton, turbidity, and macrophytes to biomanipulation in a shallow prairie lake. Canadian Journal of Fisheries and Aquatic Sciences 51:1180–1188.

Hanson, M. A., B. R. Herwig, K. D. Zimmer, and N. Hansel-Welch. 2017. Rehabilitation of shallow lakes: time to adjust expectations? Hydrobiologia 787:45–59.

Hargeby, A., G. Andersson, I. Blindow, and S. Johansson. 1994. Trophic web structure in a shallow eutrophic lake during a dominance shift from phytoplankton to submerged macrophytes. Hydrobiologia 279–280:83–90.

Hobbs, W. O., J. M. R. Hobbs, T. Lafrançois, K. D. Zimmer, K. M. Theissen, M. B. Edlund, N. Michelutti, M. G. Butler, M. A. Hanson, and T. J. Carlson. 2012. A 200-year perspective on alternative stable state theory and lake management from a biomanipulated shallow lake. Ecological Applications 22:1483–1496.

Jeppesen, E., M. Søndergaard, H. S. Jensen, and A.-M. Ventäla. 2009. Lake and reservoir management. Pages 295–309 *in* G. E. Likens, editor. Encyclopedia of Inland Waters. Academic Press.

Johnson, P. T. J., and J. M. Chase. 2004. Parasites in the food web: linking amphibian malformations and aquatic eutrophication. Ecology Letters 7:521–526.

Meijer, M. L., E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, E. Lammens, E. van Nes, J. A.

van Berkum, G. J. de Jong, B. A. Faafeng, and J. P. Jensen. 1994. Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. Hydrobiologia 275–276:457–466.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Page 125Proceedings of the 3rd International Workshop on Distributed Statistical Computing. Technische Universit at Wien.

Ramstack Hobbs, J. M., W. O. Hobbs, M. B. Edlund, K. D. Zimmer, K. M. Theissen, N. Hoidal, L. M. Domine, M. A. Hanson, B. R. Herwig, and J. B. Cotner. 2016. The legacy of large regime shifts in shallow lakes. Ecological Applications 26:2662–2676.

Scheffer, M. 1998. Ecology of Shallow Lakes. Chapman and Hall, London.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends in Ecology and Evolution 18:648–656.

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in ecology & evolution 8:275–9.

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506–509:135–145.

Søndergaard, M., E. Jeppesen, T. L. Lauridsen, C. Skov, E. H. Van Nes, R. Roijackers, E. Lammens, and R. Portielje. 2007. Lake restoration: successes, failures and long-term effects. Journal of Applied Ecology 44:1095–1105.

Su, Y. and M. Yajima. 2015. R2jags: A package for running jags from R. R package version 0.05-01. http://CRAN.R-project.org/package=R2jags

Vitense, K., J. Fieberg, N. Hansel-Welch, M. A. Hanson, B. R. Herwig, and K. D. Zimmer.. 2016 Shallow lakes in Minnesota: Can we predict future conditions? Pages 231-242 in L. Cornicelli, M. Carstensen, G. D'Angelo, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings, 2015. Minnesota Department of Natural Resources, Wildlife Populations and Research Unit, St. Paul, Minnesota, USA.

Wang, H. J., H. Z. Wang, X. M. Liang, and S. K. Wu. 2014. Total phosphorus thresholds for regime shifts are nearly equal in subtropical and temperate shallow lakes with moderate depths and areas. Freshwater Biology 59:1659–1671.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2003. Relationships among nutrients, phytoplankton, macrophytes, and fish in prairie wetlands. Canadian Journal of Fisheries and Aquatic Sciences 60:721–730.

Zimmer, K. D., M. A. Hanson, B. R. Herwig, and M. L. Konsti. 2009. Thresholds and stability of alternative regimes in shallow prairie-parkland lakes of central north America. Ecosystems 12:843–852.

Table 1. Estimated total phosphorus (TP) thresholds with 95% credible intervals from the fit of Bayesian latent variable regression models to 3 different years (2009-2011) of shallow lake data collected in July in Minnesota, USA. These thresholds determine which lake states are possible for a specific value of TP (only the clear state is possible when TP is less than the lower threshold, only the turbid state is possible when TP is higher than the upper threshold, and either state is possible for TP values between the 2 thresholds). The model fit to all 3 years of data included random logistic intercepts for each lake.

Year	Lower TP threshold (μg/L)	Upper TP threshold (μg/L)
2009	96.03 (41.87, 107.82)	434.93 (410.94, 644.15)
2010	49.97 (32.61, 124.21)	350.01 (330.02, 639.69)
2011	30.27 (19.22, 50.97)	366.36 (341.68, 622.97)
All Years	44.29 (42.30, 52.29)	437.03 (410.42, 480.20)

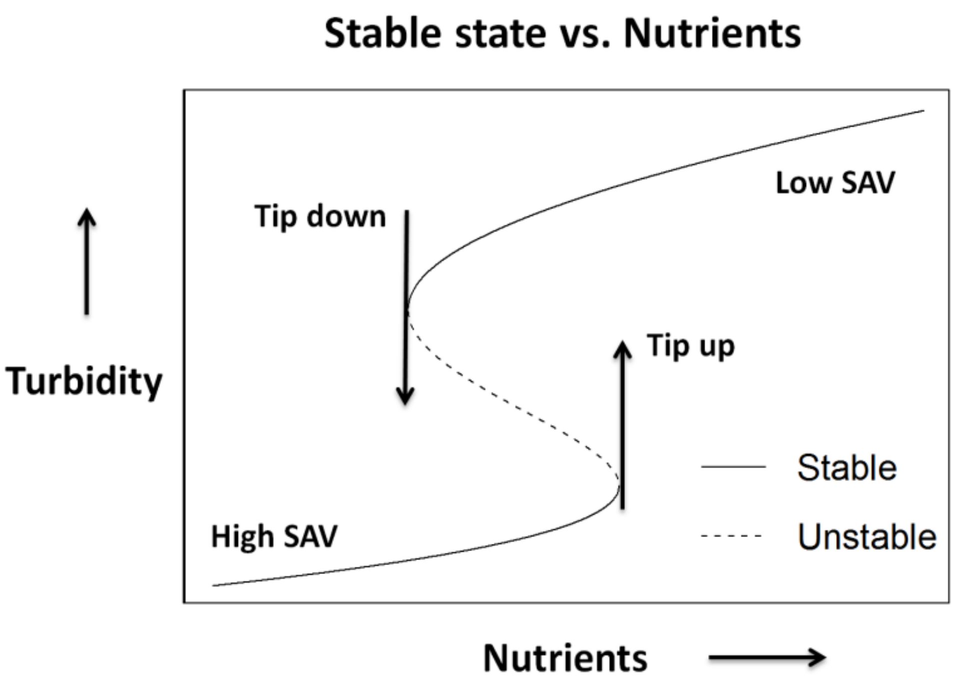

Figure 1. Bifurcation diagram from a theoretical model describing shallow lake dynamics. At low nutrient levels (left of "tip down" threshold), only the clear stable state exists (lower solid line). At high nutrient levels (right of the "tip up" threshold), only the turbid stable state exists (upper solid line). In between the 2 thresholds, 2 different stable states are possible under the same nutrient conditions, depending on whether initial turbidity levels lie above or below the unstable state (dotted lie) in this region of bistability.

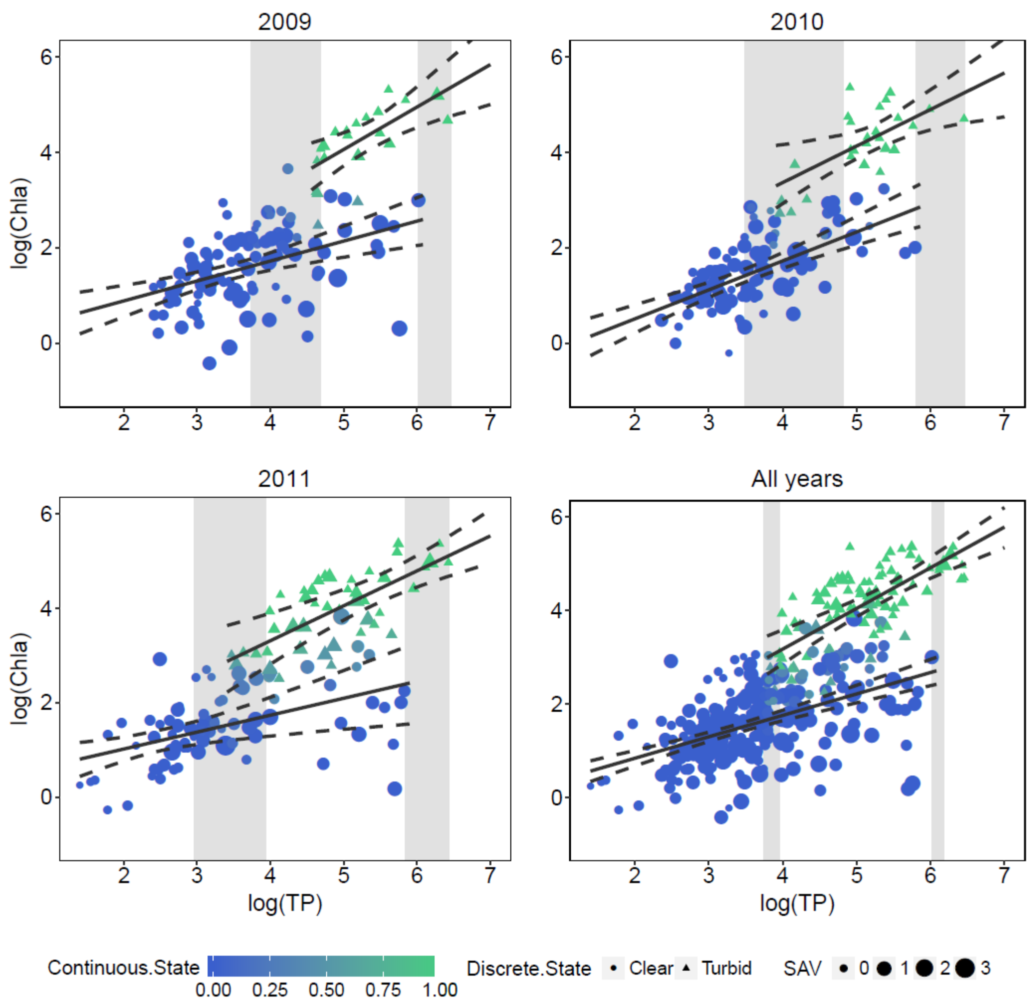

Figure 2. Bayesian latent variable regression (BLR) estimated steady state relationships between total phosphorus (TP) and chlorophyll *a* (Chla) for 3 different years (2009-2011) of shallow lake data collected in July in Minnesota, USA. Black solid (dashed) lines represent average (2.5th, 97.5th quantiles) estimated steady state relationships across all Markov chain Monte Carlo (MCMC) samples. Steady state lines end at the TP threshold point estimates, and gray bands represent 95% credible intervals for TP thresholds. Circular points represent lakes classified as clear (>50% of MCMC sampled states were clear), and triangular points represent lakes classified as turbid (>50% of MCMC sampled states were turbid). The average MCMC sampled state for each lake is shown on a blue to green color gradient (0=clear, 1=turbid). Point size is proportional to submerged aquatic vegetation (SAV, units: average kg/sample). The model fit to all 3 years of data included random logistic intercepts for each lake.

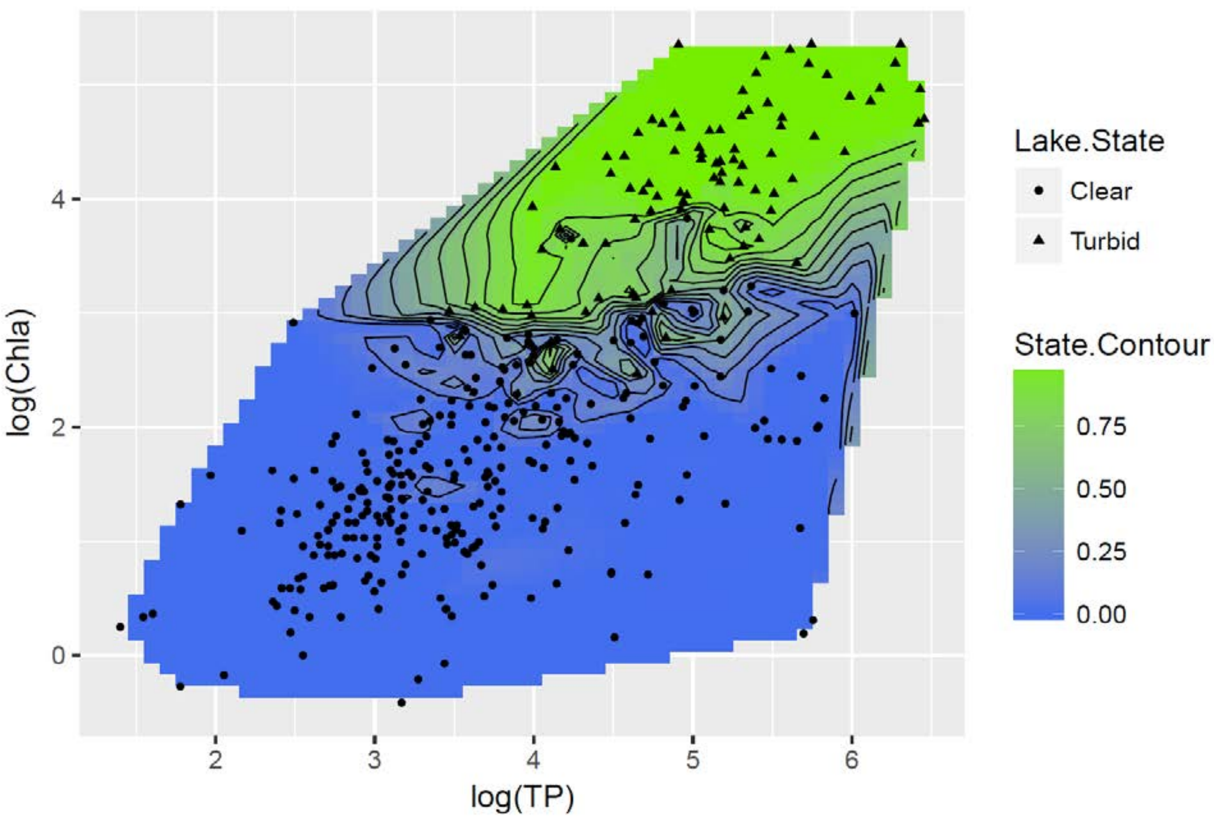

Figure 3. Heat map of all lake-year state classifications from separate fits to 3 different years (2009-2011) of shallow lake data collected in July in Minnesota, USA. Lakes are more frequently classified as clear (turbid) in blue (green) regions, where 0=clear and 1=turbid. The heat map was created using each lake's state on a continuous scale from 0-1 representing the proportion of Markov chain Monte Carlo (MCMC) samples in which the